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Short-term responses of shrub layer communities to dry season fires and tree thinning in semi-arid miombo woodlands of north-western Zimbabwe

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Short-term responses of shrub layer communities to dry season fires and tree-thinning were investigated in semi-arid miombo woodlands in North-western Zimbabwe. Fifty-four (54) plots, 50 x 50 m each, were demarcated at three miombo sites. Treatments applied were: no burn, no tree thinning; no burn, thinned; early burn, no thinning; early burn, thinned; late burn, no thinning; late burn, thinned. After three years, height structure of the shrub layer communities had significantly changed, with increases in proportions of plants below 10 cm in burnt plots due to height reductions of burnt plants and additions from natural recruitment. Non-burnt plants significantly increased in heights while frequent burning kept plants in a fire-trap. Reductions in heights were further exacerbated by herbivore browsing of new resprouts. Numbers of stems significantly increased in late burnt plants. This is a survival strategy inherent in the life history characteristics of plants in fire-prone environments to ensure quick re-establishment and regain their above-ground biomass for survival. Changes in heights of selected individual samplings did not differ among sites or between thinning treatments while burning led to increases in stems. *Monotes glaber* and *Pseudolachnostylis maprouneifolia* had above-average height increases. Mortality was low with only 5.1% in late-burnt, thinned plots, indicating good tolerance to fire.

Key words: Fire, miombo woodland, shrub dynamics, Sengwa, tree-thinning, Zimbabwe.

INTRODUCTION

The structure and dynamics of savanna ecosystems are influenced by a number of primary and secondary determinants including fire. Fire has been a common phenomenon in these ecosystems such that it has significantly influenced their functioning for millennia. The fire regime of a particular region, defined by its intensity, frequency and timing, is largely determined by grass productivity (which itself is a function of rainfall) and local grazing regimes. Frequent fires are detrimental to the development of woody plants while long fire-free periods and complete fire protection tend to promote woody plant development. Short fire-free intervals in tree and shrub communities usually result in low severity fires due to low grass production (Govender et al., 2006). Where fires are less frequent and/or of low intensity, there is often an increase in shrub development (Kruger, 1984; Smit et al., 2010). Thickets have developed in areas that either experienced less or no fires, or were overgrazed (Lock, 1993), a situation often referred to as ‘bush encroachment’ (Skowno et al., 1999; Archer, 1990; van Wilgen et

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al.,1990).

Fire causes various forms of damage to plants and its effects are more pronounced in lower vegetation strata such as shrubs, saplings and small trees. The ability of plants to survive the effects of fire is therefore an important attribute. Inherent abilities of plants to survive a fire depend on their tolerance to heat and resistance to fire (De Bano et al., 1998). Severe or more frequent fires can cause plant mortality, particularly of seedlings, shrubs and saplings whose fire tolerance levels may be generally low. Plant responses to fires are varied and largely depend on the intensity, timing and frequency of fires and the plant's life history characteristics. Re-sprouting is one of the common responses of plants to burning and this can take place from rootstocks, lignotubers, stems and/or branches.

Whilst the effects of fire on floristic composition may be difficult to interpret due to the complex interactions with rainfall, drought, herbivory and differences in species sensitivities (Frost and Robertson, 1987; Levick et al., 2012), effects of tree thinning are expected to trigger systematic responses (Thomas et al., 1999). Removal of trees affects the understorey layer by increasing light availability and may lead to increases in water and nutrient availability to the understorey plants. It is widely accepted that understorey cover increases with canopy openness (Thomas et al., 1999). By increasing available resources, tree thinning could allow a greater number of understorey species to persist. However, Alaback and Herman (1988) argued that thinning may also result in increased dominance by one or a few understorey species thereby reducing diversity.

In Sengwa Wildlife Research Area (SWRA) in north-western Zimbabwe, annual hazard-reduction burning of peripheral areas of the park has been undertaken for more than three decades for reasons of fire protection. Burnt areas were mainly parts of miombo woodland which forms about 25% of the vegetation cover. The objective of peripheral burning was to reduce cases of fire entering the area from adjacent communal lands. Whilst this objective was largely achieved (Mapaure et al., 2009), no data exist on the current or likely future ecological impacts of maintaining frequent fires within the periphery of the area, particularly on species composition, richness, diversity and structure of the lower vegetation strata. Implications of woodland thinning by elephants on lower vegetation strata need to be further explored.

This study therefore, aimed to investigate short-term responses of saplings to early and late dry season fires and tree thinning (simulating elephant impacts). It was hypothesised that dry season fires curtail recruitment of woody plants resulting in changes in the structure of the shrub/sapling layer, with more severe undesirable consequences in thinned-late burnt plots and non-thinned, non-burnt plots.

MATERIALS AND METHODS

Description of study area

The study was carried out in Sengwa Wildlife Research Area (SWRA) in north-western Zimbabwe (Figure 1). SWRA lies between 28°03′ and 28°20′E and 18°0′and 18°13′S, covering an area of 373 km^2. It is bounded by communal lands on all but the northern side, where it shares a boundary with Chirisa Safari Area, a state protected hunting area. The area experiences three climatic seasons: a hot wet period from November to April, a cool dry period from May to July and a hot dry period from August to October. Mean annual rainfall was 642 mm while mean annual temperature was 23.6°C. October is the hottest month and July is the coldest. Altitude varies from 808 to 1043 m. The area is drained by three major rivers, the Sengwa, Manyoni and Lutope. Two main soil types occur, one formed on sandstones of the Escarpment Grits and another formed on mudstones (Selibas, 1974; Bennett et al., 1983). The vegetation is generally deciduous *Brachystegia-Julbernardia* (miombo) woodland on sandy soils and dry early deciduous woodland dominated by *Colophospermum mopane* on the lower-lying heavier soils. Other vegetation types include riverine *Acacia* woodlands and mixed *Combretum* thickets on sands. These habitats are home to a diverse large mammal community of seven species of large carnivores and 18 species of large herbivores.

Experimental design

Three miombo woodland sites were selected for demarcation of plots, one in the north, one in the east and another in the south of SWRA. These sites are respectively referred to as Samapakwa (K), Airstrip (C) and Rongaronga (D) (Figure 1). They were chosen on the basis of being typical miombo woodlands among all patches of miombo in the area. At each site, 18 plots were demarcated, each measuring 50 m x 50 m, arranged in three blocks of six plots each. The blocks were arranged across a gradient and blocking was based on slope. Blocks of plots were separated by fire guards measuring 5 m wide, and the plots within each block were separated by a fire guard of the same width. All woody plants were cut just above ground level and removed from the fire guards. Fire guards were cleared of woody re-growth and herbaceous plants every year over a period of three years.

Combinations of treatments applied to plots were two fire timings (early and late dry season burns done in May and October, respectively) and two tree density levels, a 50% reduction of the original density (thinned) and a non-thinned treatment. Treatment combinations were: no burn and no thinning (NBNT - the control); no burn and thinned (NBT); early burn and no thinning (EBNT); early burn and thinned (EBT); late burn and no thinning (LBNT), and late burn and thinned (LBT). Thinning was done by evenly cutting and removing 50% of the trees form the affected plots. Treatments were randomly assigned to plots at the start of the study period and were replicated three times at each site. The burning treatments were repeated in the same plots annually but thinning was only done once at the beginning of the experiment. Plots were not protected from herbivores.

Monitoring and assessment of plants

General assessments of the structure of the shrub layer (before and after treatments) were done in belt transects each measuring 2 m x 50 m demarcated at random positions along the long axes of each plot. Within each belt transect all shrubs and saplings were assessed. The height of each shrub/sapling was measured and the

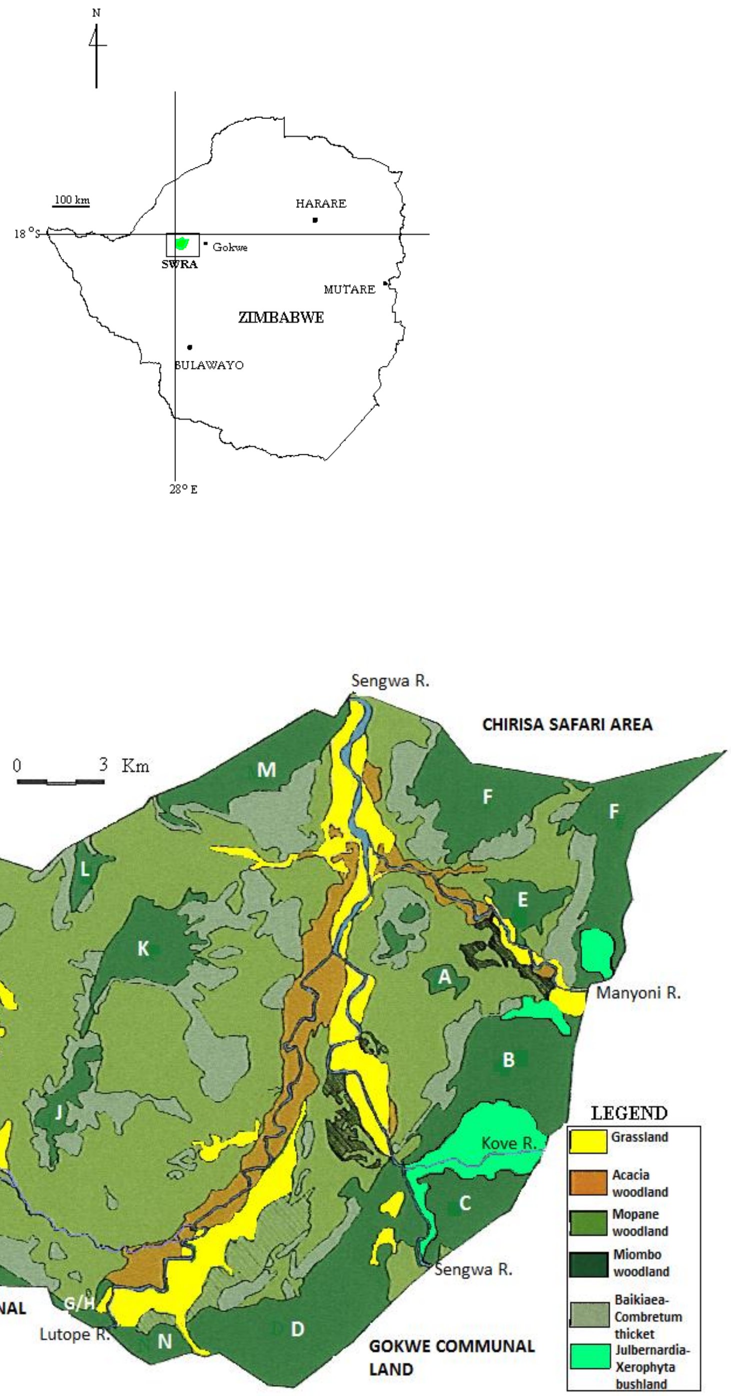


Figure 1. Location of Sengwa Wildlife Research Area (SWRA) in north-western Zimbabwe and a detailed vegetation map of the area (Patches of miombo woodland are labelled A - M).

number of stems counted. In addition, between 20 and 25 randomly selected saplings of common woody species were tagged in each plot at each site for monitoring. A total of 1164 saplings were tagged for monitoring. Tagging was done by means of metal strips engraved with identification numbers and attached to pieces of thick wire, 20-30 cm long, which were thrust into the ground next to bases of individual plants. The height of each plant was measured and the number of stems was counted. The presence of any browsing was noted and dead saplings were counted during re-assessments. Species monitored were *Brachystegia boehmii*, *Brachystegia spiciformis*, *Burkea africana*, *Erythrophleum africanum*, *Julbernardia globiflora*, *Monotes glaber*, *Ochna pulchra*, *Pseudolachnostylis maprouneifolia*, and *Terminalia sericea*. Re-assessments were done three years after initial baseline assessments.

Data analyses

Differences in the responses of the plant species to the treatments were tested using General Linear Model (GLM) ANOVA, with thinning, early burning and late burning entered as nominal continuous variables using integer scores of 0, 1 and 2 (0 - no thinning, no burning; 1- thinned, early burnt; 2 - late burnt). Response variables were changes in sapling heights and numbers of stems. Interactive effects of the treatments were included for testing in the GLM ANOVA model. Changes in height class distributions (of all shrubs/saplings) over the experimental period were tested using a χ^2 test. Height classes used were: <10, 10-20, 20-50, 50-100, 100-150, 150-200, 200-250, and >250 cm. For comparisons of individual species responses, GLM ANOVA was used for five species only (*B. boehmii*, *B. africana*, *J. globiflora*, *M. glaber* and *P. maprouneifolia*) because these were common to all sites. Sapling mortality was calculated in terms of proportions of dead plants relative to the original number of live plants in the respective treatments.

RESULTS

Changes in numbers of stems and heights

Overall changes in numbers of stems of the whole shrub/sapling community significantly differed among sites ($F = 414.39$, $df = 2$, $p < 0.001$), with significantly higher changes at Samapakwa than at the other two sites. Burning led to significant increases in numbers of stems ($F = 65.46$, $df = 2$, $p < 0.001$), and thinning had a similar effect on stems ($F = 30.32$, $df = 1$, $p < 0.001$) (Figure 2a). Changes in numbers of stems were significantly influenced by the following interactions: site x burn ($F = 12.29$, $df = 4$, $p < 0.001$; higher increases at Samapakwa with burning), site x thin ($F = 15.99$, $df = 2$, $p < 0.001$; higher increases at Samapakwa with thinning), and burn x thin ($F = 18.35$, $df = 2$, $p < 0.001$; higher increases in LBT plots) (Figure 2b). Burning significantly reduced plant heights ($F = 87.59$, $df = 2$, $p < 0.001$) while thinning led to significant increases in heights ($F = 150.28$, $df = 1$, $p < 0.001$) (Figure 3a). Interactive effects of site x burn ($F = 35.22$, $df = 4$, $p < 0.001$), site x thin ($F = 24.24$, $df = 2$, $p < 0.001$) and burn x thin ($F = 58.21$, $df = 2$, $p < 0.001$) all significantly influenced plant height responses (Figure 3b).

Since changes in overall plant heights significantly differed among sites, changes in height class distributions are presented on a per site basis. At Airstrip (Figure 4a), there were significant changes in the height class distribution in late-burnt (LB) plots, with higher changes in thinned (LBT) plots ($\chi^2 = 25.66$, $df = 5$, $p < 0.001$), non-thinned plots (LBNT) ($\chi^2 = 21.00$, $df = 5$, $p < 0.01$), with notable increases in proportions of plants <10 cm in height over the three years. Changes in height class distribution were also significant in early burnt, non-thinned (EBNT) plots ($\chi^2 = 18.21$, $df = 4$, $p < 0.01$) and in non-burnt, non-thinned (NBNT) plots ($\chi^2 = 16.28$, $df = 5$, $p < 0.01$). There was also an increase in proportions of plants <10 cm in height. The height class distribution of shrubs at Rongaronga changed significantly in EBT ($\chi^2 = 20.30$, $df = 4$, $p < 0.001$) and in LBNT ($\chi^2 = 19.40$, $df = 4$, $p < 0.001$) plots (Figure 4b), with notable increases in proportions of plants <10 cm in height and decreases in proportions of plants in the 50 to 200 cm range in burnt plots. Changes in NBT plots were also significant ($\chi^2 = 15.26$, $df = 6$, $p < 0.05$) with notable recruitment of plants into higher classes. At Samapakwa, changes in height class distributions were not significant in all treatments (Figure 4c). There were, however, decreases in proportions of plants in the 100 to 150 cm range in burnt plots.

Sapling mortality

Of the 977 saplings positively identified after 3 years, 30 had died, all of which were in burnt plots except one. The majority (66.7%) of dead saplings were at Airstrip site, while 13.3and 20% were at Rongaronga and Samapakwa, respectively. Sapling mortality was generally low, ranging from zero in non-burnt plots to 5.1% in late-burnt thinned plots (Table 1). *J. globiflora* suffered the heaviest mortality (53.3% of all dead saplings), all with a mean height of less than 50 cm. Mortality of *B. boehmii* was second (16.7% of all dead saplings) followed by *B. spiciformis* (10%), with respective mean heights below 60 cm and above 120 cm. Other species which died were *C. spinosa, P. maprouneifolia*, *O. pulchra*, *T. sericea* (each 3.3%) and *E. africanum* (6.8%).

Changes in heights and numbers of stems of selected species

Changes in heights of five common species (*B. boehmii, B. africana*, *J. globiflora*, *M. glaber* and *P. maprouneifolia*) were not significantly different among sites or between thinning treatments but were significantly different among burning treatments ($F = 11.97$, $df = 2$, $p < 0.001$) with non-burnt saplings increasing in height while burnt saplings registered little growth, particularly in late burnt plots (Figure 5a). There were no significant differences in changes in height among species. The interactive effects of site and burn were significant ($F = 2.73$, $df = 4$, $p < 0.05$) with reductions in heights at Samapakwa in early burnt plots (Figure 5b). Numbers of stems of five selected species significantly increased with late burning ($F = 20.29$, $df = 2$, $p < 0.001$) (Figure 6a) but they were not

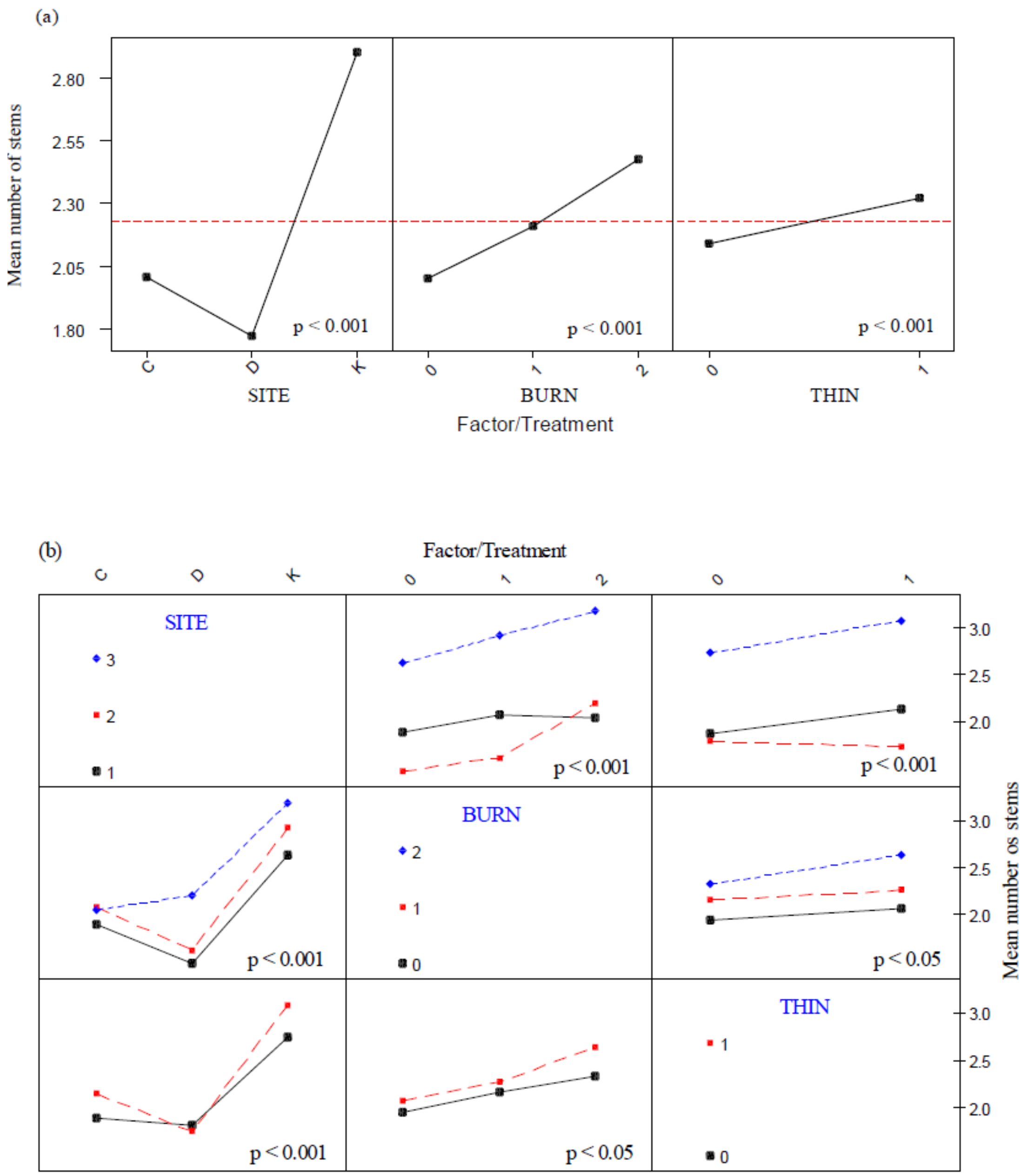


Figure 2. Main effects plots (a) and interactions plots (b) indicating the effects of site (C = Airstrip, D = Rongaronga, K = Samapakwa), burning (0 = no burn, 1 = early burnt, 2 = late burnt) and thinning (0 = no thinning, 1 = thinned) on the mean number of stems per plant (significance levels are shown in the respective graphs; NS = not significant)

significantly influenced by interactive effects between any two factors (Figure 6b). Site and thinning did not significantly influence numbers of stems. There were significant differences in changes in numbers of stems among species ($F = 4.40$, $df = 4$, $p < 0.01$), with above average increases in *M. glaber* and *P. maprouneifolia*. *B. boehmii*, *B. africana* and *J. globiflora* registered below-average increases in number of stems.

DISCUSSION

There were significant increases in numbers of stems with late burning and/or thinning, a result consistent with hypothesized trends. Woody plants in arid and semi-arid areas may respond to burning in various ways including resprouting or death followed by mass germination if there is adequate post-fire rain (Griffin and Friedel, 1984).

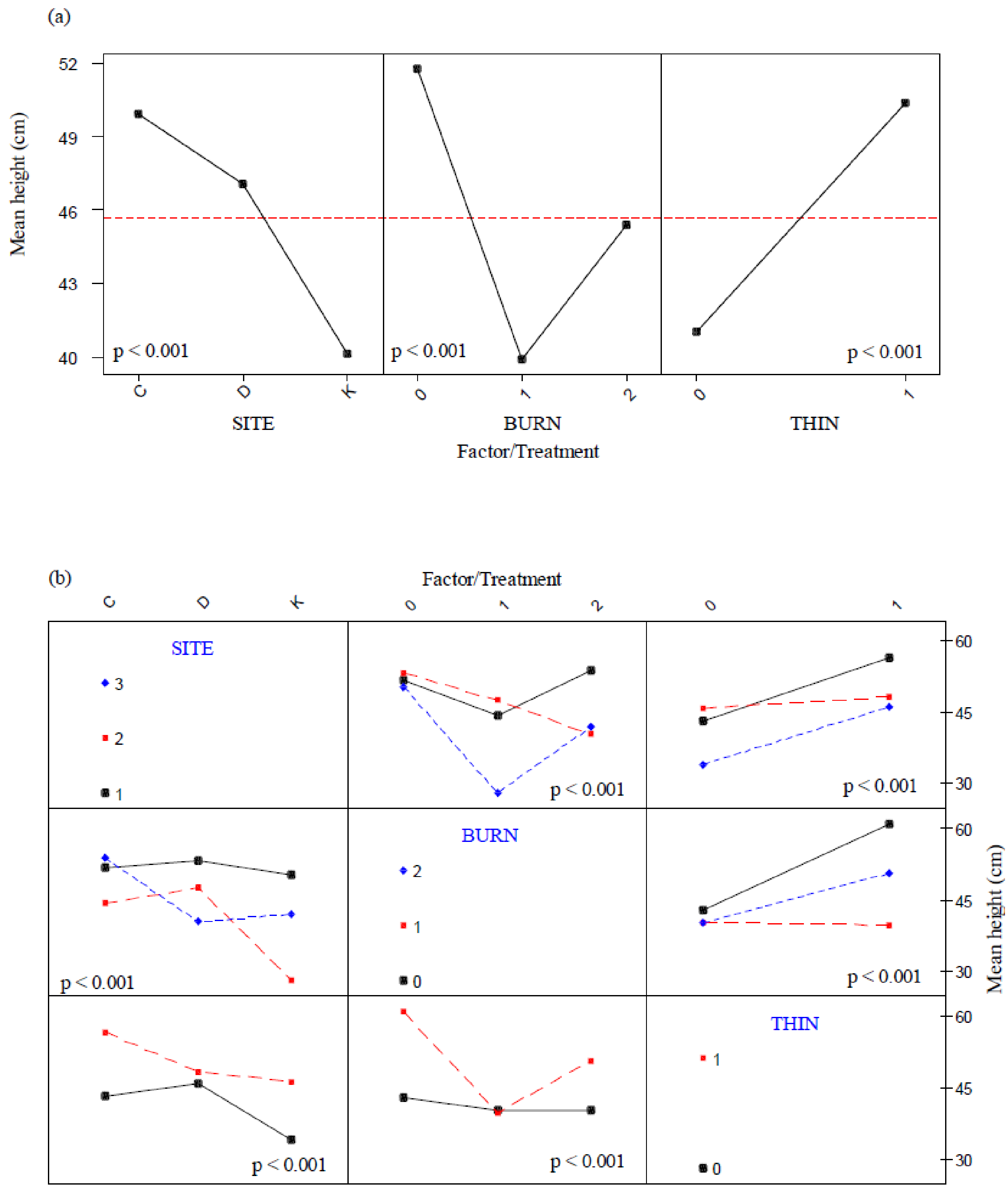


Figure 3. Main effects plots (a) and interactions plots (b) indicating the effects of site (C = Airstrip, D = Rongaronga, K = Samapakwa), burning (0 = no burn, 1 = early burnt, 2 = late burnt) and thinning (0 = no thinning, 1 = thinned) on the mean heights of shrubs (significance levels are shown in the respective graphs; NS = not significant)

Plants may also be induced to produce resprouts when the terminal meristem is damaged, irrespective of the damage agent. However, significant differences in numbers of stems among sites may be indicative of site-specific responses of plants. This may be a consequence of differences in species composition, site conditions and burn severity among sites. After-burn inspections indicated that some plants in burnt plots were unaffected by fire since they ‘escaped’ in islands where grass biomass was either low or absent. The responses of such

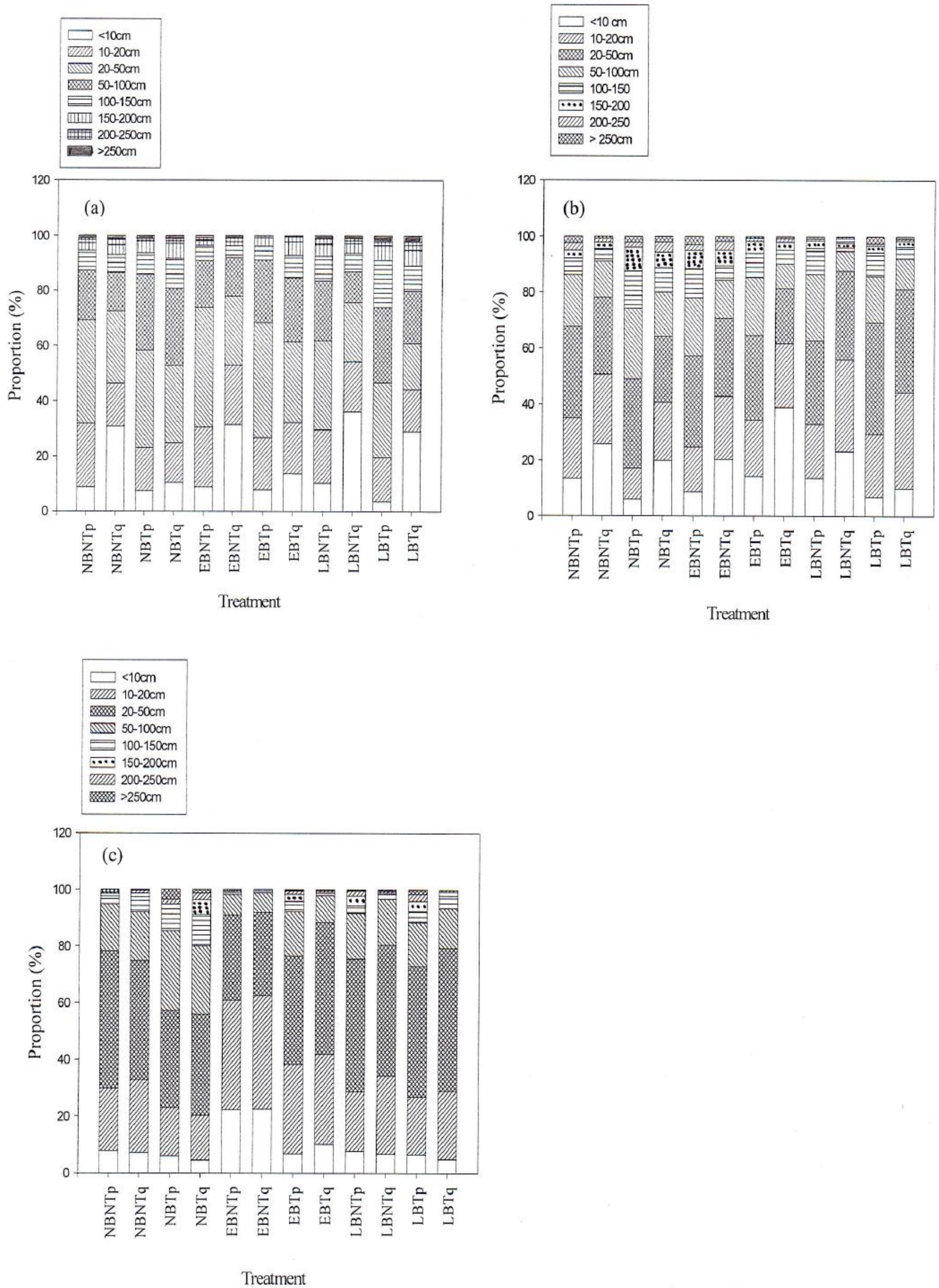


Figure 4. Changes in height class distribution patterns of shrubs and saplings at Airstrip (a), Rongaronga (b) and Samapakwa (c) at the start of the experiment (p) and 3 years later (q). NB = not burnt, EB = early burnt, LB = late burnt, NT = not thinned. T = thinned.

Table 1. Summary of sapling mortality indicating numbers of saplings and their original mean heights subjected to different burning and thinning treatments (NBNT = non-burnt, not thinned; NBT = non-burnt, thinned; EBNT = early burnt, not thinned; EBT = early burnt, thinned; LBNT = late burnt, not thinned, LBT = late burnt, thinned). All 5 species are combined.

Treatment	**Number of experimental saplings (n)**	**Number of dead saplings**	**Mortality after 3 years (%)**	**Original height of dead plants (cm) (mean ±SE)**
NBNT	177	1	0.6	68.0 (±0.0)
NBT	165	0	0.0	N/A
EBNT	159	7	4.4	58.1 (±13.4)
EBT	149	7	4.7	73.9 (±23.5)
LBNT	170	7	4.1	65.6 (±19.4)
LBT	157	8	5.1	42.0 (±4.9)
Total/overall	977	30	3.1	59.6 (±7.8)

plants would be similar to those under no burn (control) conditions. Increases in numbers of stems due to burning significantly differed among species. *M. glaber* and *P. maprouneifolia* registered above-average increases in numbers of stems. These results are indicative of individualistic, species-specific responses to fire, which was dependent on site. This underlines the importance of local interactions among abiotic and biotic factors in influencing small-scale patterns of individual plant responses to fire in semi-arid environments. This could be brought about by the fire history of each site prior to the experiment. Samapakwa (site K) experienced relatively low fire frequencies compared to Airstrip (site C) and Rongaronga (site D) (Mapaure et al., 2009). Frost (1999a) indicated that in *B. africana* and *T. sericea*, numbers of basal sprouts decreased (after an initial increase) with successive fire events, and attributed the initial increase to a mechanism of maximising carbon gain by plants.

Under conditions of severe fire, resprouting provides a selective advantage to plants, enabling them to quickly re-establish themselves and have competitive advantage over plants which regenerate from seed only (Keeley et al., 1999; Moreira et al., 2012). Increases in the numbers of stems with fire ensures that, through mobilisation of resources from rootstocks or lignotubers, plants regain their above-ground biomass in relatively short time to ensure their survival. In the absence of fire, species that survive by vegetative regeneration from the rootstocks are capable of continuously regenerating their canopy with basal sprouts (Keeley, 1992).

Burning significantly reduced plant heights while thinning led to significant increases in their heights. Interactions among treatments also significantly influenced height responses of plants. Whereas reductions in heights in burnt plots were largely due to top-kill by fire, height decreases in non-burnt plots were due to large mammal browsing. Most *Brachystegia boehmii* and *Burkea africana* saplings were heavily browsed resulting in significant height reductions. Large mammalian herbivores tend to prefer tender, nutritious leaves and shoots such as resprouts due to their high palatability (Holt and Coventry, 1990; Dörgeloh, 1999; Moe et al., 1990). *Brachystegia boehmii* was most affected by elephant browsing, an observation which could further explain its local disappearance from some sites in the area observed by Mapaure and Moe (2009). Frost (1999b) indicated that in drier environments, it was not important whether a fire was early or late but its presence or lack of it made an important difference. This assertion is supported by results of this study where the differences in effects of early and late burns were minimal but only significant between burnt and non-burnt saplings. Belsky (1984) reported similar results where mean heights of tree saplings were significantly reduced by browsing in Serengeti National Park, Tanzania. Height reductions through browsing could outweigh height increases in non-browsed shrubs and saplings resulting in net height reductions recorded during the study.

Observations soon after fire indicated that some plants particularly lower height classes were burnt to ground level but their basal resprouts had reached considerable heights at the time of re-assessments. This was particularly true for *C. spinosa*. In Serengeti National Park, 92 and 68% shrubs less than 1 m and 1-2 m in height, respectively, were burnt back to ground level during fires (Norton-Griffiths, 1979), an observation supporting current findings. Increases in heights after tree thinning can be explained by the reduction in above-ground competition between shrubs/saplings and small trees.

The mean plant height was higher in late burnt than early burnt plots, a finding contrary to expectation. Elsewhere, it was however shown that shrubs resprouting after high intensity fires (often characteristic of late dry season burns) had substantially higher rates of shoot elongation than after low intensity fires (Hodgkinson, 1992). This was influenced by above-average precipitation received after the October burn during the experimental period, resulting in improved shoot regrowth.

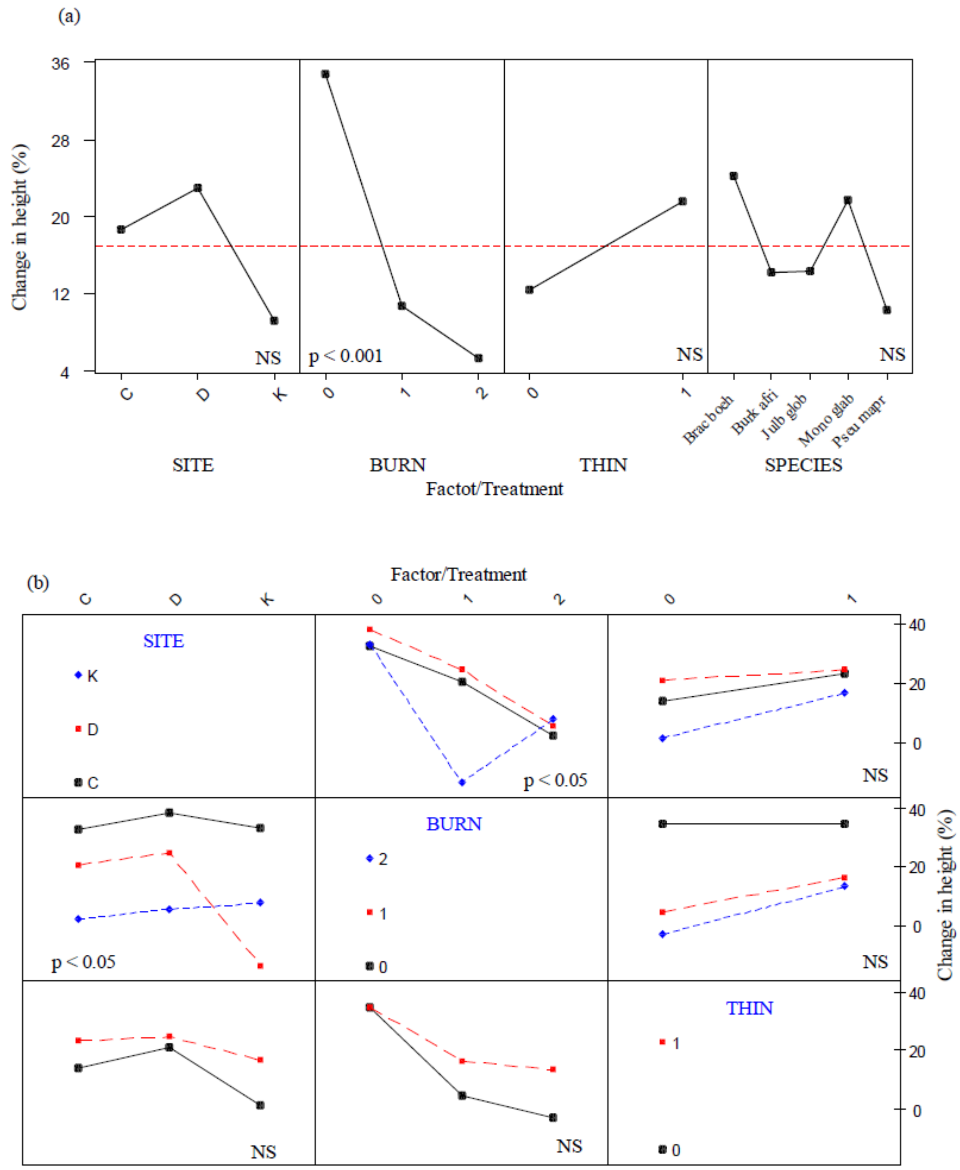
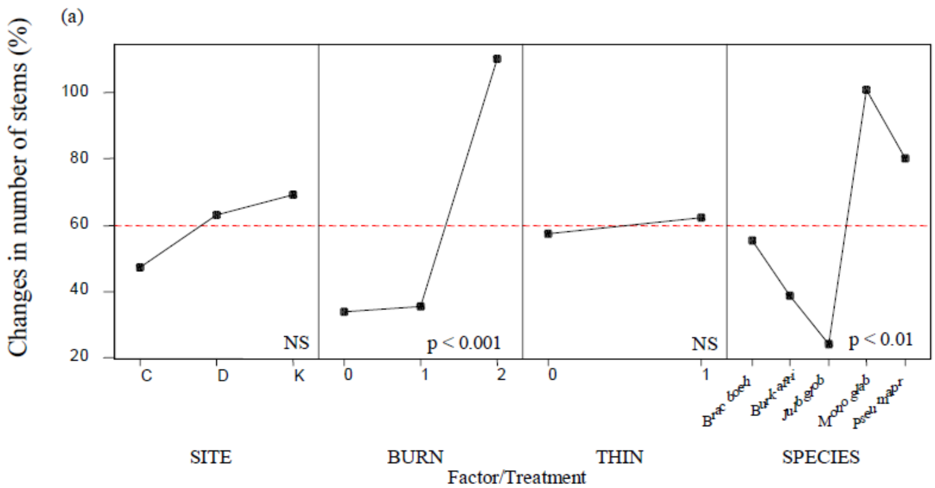


Figure 5. Main effects plots (a) and interactions plots (b) indicating the effects of site (C = Airstrip, D = Rongaronga, K = Samapakwa), burning (0 = no burn, 1 = early burnt, 2 = late burnt) and thinning (0 = no thinning, 1 = thinned) on mean heights of saplings of five common species (Brac boeh = *Brachystegia boehmii*, Burk afri = *Burkea africana*, Julb glob = *Julbernardia globiflora*, Mono glab = *Monotes glaber* and Pseu mapr = *Pseudolachnostylis maprouneifolia*) (Significance levels are shown in the respective graphs; NS = not significant)

Height class distributions indicate a clearer picture of changes in vertical structure of shrub/sapling communities. Increases in relative proportions of plants in lower height classes (<10, 10 to 20 cm) were due to a combination of two processes: First, a net recruitment of new seedlings, particularly *E. africanun* and *J. globiflora*, which led to large increases in numbers of small plants (irrespective of treatment) during the rainy season. Second, plants that were burnt back or top-killed were reduced to lower height classes leading to increases in proportions of plants in the lower height classes. This is consistent with the observation by Griffin and Friedel (1984) who reported significant differences in structure of shrub layers burnt in either season compared to that of non-burnt controls.

There was a consistent height reduction in the range 50-100 cm in non-burnt plots, which can be attributed to browsing. Browsing within this height range was probably



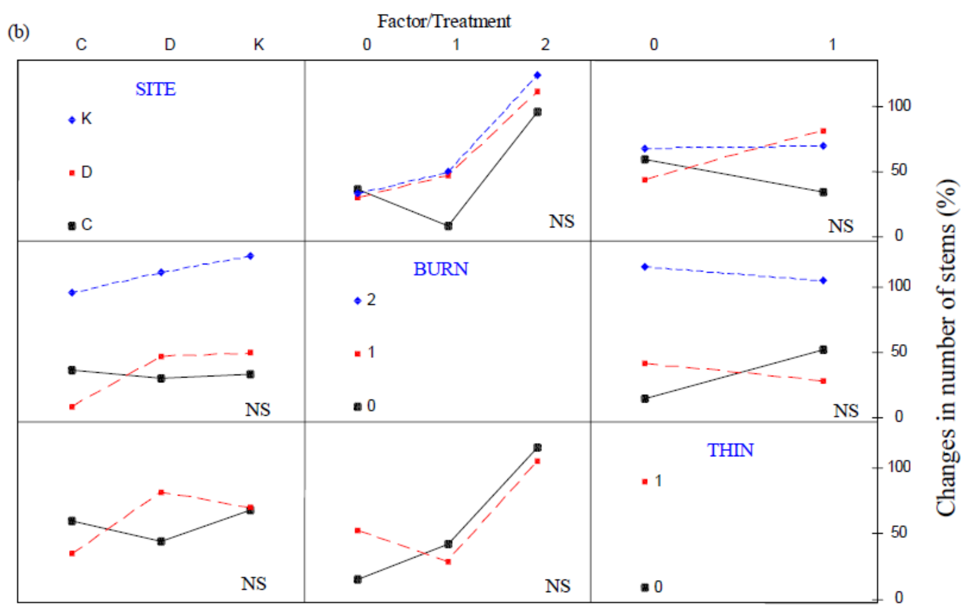


Figure 6. Main effects plots (a) and interactions plots (b) indicating the effects of site (C = Airstrip, D = Rongaronga, K = Samapakwa), burning (0 = no burn, 1 = early burnt, 2 = late burnt) and thinning (0 = no thinning, 1 = thinned) on number of stems of saplings of five common species (Brach boeh = *Brachystegia boehmii*, Burk afri = *Burkea africana*, Julb glob = *Julbernardia globiflora*, Mono glab = *Monotes glaber* and Pseu mapr = *Pseudolachnostylis maprouneifolia*) (Significance levels are shown in the respective graphs; NS = not significant)

by smaller mammals (such as impala) rather than elephants as the latter browse mainly between 1 and 2m (Guy, 1976; Belsky, 1984).

These observations therefore imply that height reductions in burnt plots were not due to fire alone but browsing had a further negative effect. Belsky (1984) showed that a combination of browsing and burning in the Serengeti National Park maintained the height of tree saplings below 30 cm for three years compared to height increases of up to more than 75 cm in non-burnt, non-browsed plots.

Plants taller than 200 cm were less affected by fire, an indication that a critical height for plants to escape fires at current fire intensities in the study area was around this value. Most shrubs and saplings were burnt back to below 50 cm, a height within which they were maintained by frequent fires. Fire-suppressed multi-stemmed plants (often referred to as `gullivers') have been shown to persist in plant communities for long periods (Bond and van Wilgen, 1996; Skowno et al., 1999; Smit et al., 2010).

If the fire-free interval increases, most ‘gullivers’ grow taller than 200cm and escape the fire trap, a scenario that may explain the increases in woody cover and densities of small trees recorded in the study area over a period of time (Mapaure and Moe, 2009). Hodgkinson (1998) noted that the proportion of plants surviving the passage of fire is determined by the height structure of each population of plant species present.

Monitoring of individual plants through time gives a relatively good indication of mortality as revealed by tagged plants in this study. Thinning of the woody component usually results in an increase in grass biomass (Knoop and Walker, 1985). This in turn leads to more intense fires, especially in the late dry season. It is therefore, expected that there would be higher reductions in heights of saplings in thinned plots, more so in thinned, late burnt plots. However, not all mortality can be attributed to fire as other factors could also have interactively caused plant death. Mortality figures presented in this paper were based only on plants whose tags could be found at the end of the experimental period, and excluded missing tags. It is therefore possible that mortality rates were either under- or over-estimated, depending on whether missed saplings were dead or alive (but not located), respectively. Griffin and Friedel (1984) reported considerable deaths of plants in the absence of fire, particularly in the smallest size-classes. Moisture stress is one of those factors that can cause significant mortality in young plants, even in the absence of fire. This probably happened at Airstrip since fire tended to be patchy at that site. Herbivore foraging on post-fire green flush may have a double effect; trampling of young plants, and heavy browsing on others, rendering them weak and sometimes resulting in death. Since all dead saplings (except one) in this study were in burnt plots, it is however; highly likely that fire was largely responsible for sapling deaths recorded in this study.

Fire-related mortality was recorded only in saplings less than a metre high, and mostly single-stemmed. If height and initial numbers of stems are cautiously taken as surrogates for age, this could indicate that dead saplings were relatively young and thus, of low fire-tolerance due to their limited below-ground biomass. *J. globiflora* and *B. boehmii* appeared particularly susceptible at this young stage compared to other species such as *M. glaber* and *P. maprouneifolia*. Despite being somewhat susceptible to fire at an early stage, *J. globiflora* and *B. boehmii* seemed tolerant once the height was above 50cm but the former species was less browsed by large mammals compared to the latter. This observation could further explain long-term increases in relative importance of *Julbernardia globiflora* reported by Mapaure and Moe (2009) in the area. Current results are consistent with observations from an Australian savanna where a high percentage of established seedlings of a number of species were killed by fire but survival increased with height reaching (depending on species) a maximum of up to 60 cm (Norton-Griffiths, 1979). Most species in savannas are easily killed by fire as seedlings and saplings. However, their resistance and tolerance increases with age up to the point where they become senescent, and again become susceptible (Kruger, 1984). Therefore, it is important for range managers of protected areas to have a holistic approach in managing the woodland-fire-herbivore system and to treat different patches of miombo woodland differently due to their varied responses to similar treatments.

Conclusions

This study has shown that the lower stratum of woody layer in semi-arid miombo woodland responds differently to fire treatments, depending on local site conditions and post-fire herbivore browsing. Thinning of the trees led to increases in heights of saplings and shrubs due to reduced above ground completion with trees. Burning, especially late burning, led to significant increases in numbers of stems through basal resprouting.

Resprouting provides a selective advantage to plants by enabling them to quickly re-establish themselves and ensures that the plants regain their above-ground biomass in a relatively short period of time to ensure their survival. Burning significantly reduced heights of plants and resulted in significant changes in the height structure of the lower woody stratum of shrubs and saplings. This is mainly due to the fact that frequent burning keeps shorter plants in a fire trap, and with natural recruitment during the wet season, there tends to be increases in proportions of shorter plants.

This study has also shown that different species may respond differently to fire, largely due to their individual life-history characteristics. Mortality of saplings due to fire was generally lower than anticipated, showing that these species are tolerant to fire and have adaptive life history characteristics to survive fires. Hence, fire management practices in semi-arid miombo woodlands must take cognisant of the differential responses of individual plant species to fire as well as differences in site characteristics the lead to differences in plant responses.

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